# Intra-annual plasticity of growth mediates drought resilience over multiple years in tropical seedling communities

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**Title: Intra-annual plasticity of growth mediates drought resilience over multiple years in tropical seedling communities**

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## Abstract

Precipitation patterns are changing across the globe causing more severe and frequent drought for many forest ecosystems. Although research has focused on the resistance of tree populations and communities to these novel precipitation regimes, resilience of forests is also contingent on recovery following drought, which remains poorly understood, especially in aseasonal tropical forests. We used rainfall exclusion shelters to manipulate the inter-annual frequency of drought for diverse seedling communities in a tropical forest and assessed resistance, recovery and resilience of seedling growth and mortality relative to everwet conditions. We found seedlings exposed to recurrent periods of drought altered their growth rates throughout the year relative to seedlings in everwet conditions. During drought periods seedlings grew slower than seedlings in everwet conditions (i.e. resistance phase) while compensating with faster growth after drought (i.e. recovery phase). However, the response to frequent drought was species dependent as some species grew significantly slower with frequent drought relative to everwet conditions while others grew faster with frequent drought due to overcompensating growth during the recovery phase. In contrast, mortality was unrelated to rainfall conditions and instead correlated with differences in light. Intra-annual plasticity of growth and increased annual growth of some species led to an overall maintenance of growth rates of tropical seedling communities in response to more frequent drought. These results suggest these communities can potentially adapt to predicted climate change scenarios and that plasticity in the growth of species, and not solely changes in mortality rates among species, may contribute to shifts in community composition under drought.

## Introduction

Forests across the globe are experiencing reduced or more variable precipitation (Forzieri *et al.*, 2014; Chadwick *et al.*, 2015) leading to increased tree dieback (Lewis *et al.*, 2011; Peng *et al.*, 2011; Steinkamp & Hickler, 2015). The response of a forest community to novel precipitation patterns is the result of the resistance and recovery of the species and individuals comprising the community (Mitchell *et al.*, 2016). Therefore, assessing both the immediate response of a forest and the overall recovery of the forest is important for understanding the long-term effects on composition and ecosystem function (Anderegg *et al.*, 2015; van der Sande *et al.*, 2016). However, most research has focused solely on the resistance phase (i.e. the immediate impacts of a drought; Potts 2003; Lewis *et al.* 2011; Rowland *et al.* 2015) with much less attention on the post-drought recovery of forest communities or legacy effects (Anderegg *et al.*, 2013, 2015; Cole *et al.*, 2014; Hartmann *et al.*, 2015), which is important for understanding long-term vegetation shifts under novel precipitation patterns (Martinez-Vilalta & Lloret, 2016).

The impact of drought on plant communities, and in turn ecosystem function, depends on the intensity, duration, timing and frequency of drought events (Mitchell *et al.*, 2016). The response of a plant community to these components of drought consists of the loss of a function during drought (i.e. resistance) and the return of the function after drought (i.e. recovery), which are the features of resilience (Lloret *et al.*, 2011; Cole *et al.*, 2014; Mitchell *et al.*, 2016). Within this concept, alterations to any of these four characteristics of drought under climate change will potentially affect ecosystem functions. However, the relative importance of these characteristics is dependent on other variables such as the community composition (i.e. traits of the species; (Li *et al.*, 2015; O'Brien *et al.*, 2017), abiotic factors (e.g. soil type; Nakagawa *et al.* 2000; Potts 2003), biotic interactions (Desprez-Loustau *et al.*, 2006; McDowell *et al.*, 2011), historical

drought regime (Cole *et al.*, 2014; Mitchell *et al.*, 2016) and post-drought environmental conditions (Lloret *et al.*, 2011, 2012)

Many forests throughout the world are shifting from communities assembled by differences in light or nutrients to communities assembled by differences in water availability (Hartmann, 2011), especially everwet tropical forests that have rarely experienced water limitation historically (Phillips *et al.*, 2010; Lewis *et al.*, 2011; Cole *et al.*, 2014). This shift in the limiting resource may alter competitive dynamics and the demographic rates of species (e.g. growth and mortality) and in turn impact species distribution and community composition (Kroiss *et al.*, 2015; Anderegg & HilleRisLambers, 2016; Martinez-Vilalta & Lloret, 2016; van der Sande *et al.*, 2016). The lowland tropical forests of Southeast Asia, especially those occurring on the relatively aseasonal island of Borneo, may be particularly sensitive to these altered precipitation patterns because rainfall is generally high and evenly distributed over the year (Walsh & Newbery, 1999; Phillips *et al.*, 2010), and drought normally occurs on relatively infrequent cycles at supra-annual intervals (Walsh & Newbery, 1999; Gibbons & Newbery, 2003; Sakai *et al.*, 2006). Experimental manipulation of the rainfall regime is a useful approach to test the effects of altered precipitation patterns on seedling communities in this everwet system, especially given the relative paucity of historical observational data relating drought and stand dynamics. Seedling communities are also important for the long-term recovery and resilience of forest ecosystems as climate change alters the overstorey composition and structure (Potts, 2003; O'Brien *et al.*, 2013). In addition, climate change alters seedling regeneration dynamics (establishment and recruitment) through interactions with herbivores and pathogens, which are drivers of community assembly processes in tropical forests (Bell *et al.*, 2006; Bagchi *et al.*, 2014). For example, drought may predispose seedlings to mortality by pathogens and

herbivores thereby enhancing vegetation shifts beyond the direct effects of drought (McDowell *et al.*, 2011).

In this study, we altered the drought frequency for seedling communities in a tropical forest that, in recent history (i.e. the last 10 – 20000 years; Heaney 1991; Bird *et al.* 2005), has primarily experienced infrequent supra-annual droughts associated with El Niño Southern Oscillation events (ENSO). We applied rainfall exclusion shelters yearly for three consecutive years to achieve water limitation similar to that measured during the 1997 – 98 ENSO event and assessed resistance and recovery of the seedling communities in response to this yearly drought return interval. Therefore, we manipulated the frequency and intensity of drought but ignored the timing of drought — which we assumed to be less important in this aseasonal tropical forest. Developed from the conceptual framework proposed by Körner (2006) with regards to $CO_2$ manipulation experiments, we propose four growth responses of seedlings to more frequent drought: 1) no effect of drought on growth, 2) an initial decline in growth followed by a compensatory recovery of growth, 3) a reduced growth followed by a recovery parallel to growth in everwet conditions or 4) a reduced and declining growth relative to seedlings in everwet conditions (see Fig. 3 in Körner 2006 for scenarios). In addition, we expected drought to increase seedling death relative to everwet conditions.

## Materials and methods

### *Site*

The experiment was conducted near the Malua Field Station (N05º05’20’’ E117º38’32’’; 102 masl) in the *c.* 33,000 hectare Malua Forest Reserve located approximately 22 km northwest of Danum Valley Field Centre in Sabah, Malaysia (Tuck *et al.*, 2016). Malua was initially logged in the mid-1980s and, except for the 500 hectare Sabah Biodiversity Experiment site, was re-

logged in 2005. Eastern Sabah has historically had an aseasonal climate and an average monthly rainfall (se) of 240 mm (33) and an average yearly total of 2900 mm (90), as recorded at Danum Valley Field Centre from 1986 to 2014. There have been severe drought events occurring irregularly since the early 1980s in the area (e.g. 1986 – 1987, 1991 – 1992 and 1997 – 1998, Walsh & Newbery 1999). The mean daily minimum temperature measured at the Malua Field Station during the experiment was 22.7° C and the mean daily maximum temperature was 31.6° C. The mean mid-day humidity was 59% and the mean night-time humidity was 95%.

*Experimental design*

In December 2011, we established 12 plots along a topographic gradient from 100 masl at a small stream to 130 masl on top of a low ridge. Soil texture across the gradient showed little variability with a mean (se) of sand, silt and clay content equal to 20% (2), 11% (1) and 65% (3), respectively. Each plot consisted of two identical sub-plots (90 x 120 cm) planted approximately 70 cm apart. We planted communities of 20 species (Supporting Information Table S1) consisting of one seedling per species in each sub-plot (40 seedlings at each paired plot and a density of 19 seedlings $m^{-2}$ per sub-plot; 480 seedlings in total). Prior to planting, competing understorey vegetation within the plot area was removed to ground level and was continuously removed during the experiment. Species were randomly assigned to a planting point in each sub-plot at 30 x 30 cm spacing. Therefore, among plots, species had unique neighbors but within plots neighbors were identical in each sub-plot. The species selected comprised seventeen species of the *Dipterocarpaceae* family, one from the *Fabaceae* family and two from the *Bombacaceae* family. The *Dipterocarpaceae* seedlings included 1 species from the genus *Dryobalanops*, 3 species from the genus *Hopea,* 2 species from the genus *Parashorea* and 11 from the genus *Shorea* (see Supporting Information Table S1 for species details). Seedlings were

134 planted from 15-month-old nursery stock, which were grown in polyethylene pots in a nursery
135 under 5% light. Seeds were sourced from Malua and adjacent forest reserves during the mast
136 fruiting event of August 2010 (O'Brien *et al.*, 2013).

137 Seedlings established for ~2 months, and during this time, no mortality was observed. In
138 February 2012, a rainfall exclusion shelter was constructed over one sub-plot in each plot. Clear
139 plastic polyethylene sheeting was used to create the shelters 1.5 m above the seedlings covering
140 approximately 1.5 x 1.8 m (i.e. an additional 30 cm of area on all sides of the plot). Aluminum
141 sheeting 10 cm high was inserted 5 cm into the soil upslope from each plot to prevent overland
142 water flow into the plots during heavy rainfall events. Exclusion shelters remained in place for
143 ~90 days and were then removed. Although 90 days seems like an excessively severe drought,
144 the natural conditions during this time remained rainy and cloudy. Therefore, 90 days were
145 necessary to simulate reduced soil water availability in the field while during a natural drought
146 soil drying would occur more rapidly. In February 2013 and 2014 the shelters were returned to
147 the same sub-plots and left for approximately 100 days for each year. During experimental
148 drought periods, control sub-plots received natural rainfall and were also given supplementary
149 irrigation (~10 L per sub-plot) in the event of no rain for 3 days. Furthermore, both sub-plots
150 were irrigated in the event of 3 days with no rainfall during the non-drought periods of the
151 experiment. This irrigation regime ensured that control sub-plots (everwet treatments) remained
152 wet relative to the rainfall excluded sub-plots (drought treatments). Neither sub-plot experienced
153 drought when rainfall exclusion shelters were not present. With this design and irrigation regime,
154 we ensured that the seedling community only experienced drought because of the rainfall
155 exclusion shelters (see Supporting Information Fig. S1 for soil water potential during the
156 experiment).

157 *Environmental conditions*

158 We measured photosynthetically active radiation using quantum sensors (SKP 210; Skye
159 instruments LTD, Llandrindod Wells, Powys, UK) in each sub-plot for 24 hours. These data
160 were compared to simultaneous measurements of direct sunlight at the Malua Field Station in
161 order to assess the light differences among plots and between sub-plots within a plot. Light was
162 similar between sub-plots but among plots light ranged from 0.3% to 13% (Supporting
163 Information Fig. S2).

164 Volumetric soil moisture content was regularly measured at the soil surface at three
165 locations in each sub-plot during the first drought and at a depth of 15 cm during the second and
166 third drought using a ML2x Theta Probe and HH2 moisture meter (Delta-T Devices, Burwell,
167 Cambridge, UK). The relationship between soil water potential and volumetric soil moisture
168 content was determined using the filter paper method (Deka *et al.*, 1995; O'Brien *et al.*, 2013).
169 At the end of the second and third drought period, we measured the mid-day leaf water potential
170 of 3 –5 seedlings of each species in everwet and drought treatments to test if seedlings were
171 responding to reduced soil water availability. We chose not to remove leaves in the first year
172 because most seedlings had very few leaves.

173 *Seedling monitoring*

174 The height of each seedling was measured at the time rainfall exclusion shelters were
175 applied (beginning in February 2012) and during removal of shelters every year for three years.
176 Height was also measured 340 days after the final period of rainfall exclusion shelters (May
177 2015). Relative growth rate (RGR) was calculated as the natural log difference in height between
178 the beginning and end of a period divided by the number of days between measurements. This
179 calculation was carried out for each period (3 periods with rainfall exclusion shelters and 3

180 periods with no rainfall exclusion shelters for a total 7 measurements including the initial
181 measurement). Dead seedlings were also recorded at each census.

182 *Statistical analysis*

183 Mean soil water potential during each drought was analyzed as a function of treatment
184 (fixed factor with 2 levels; drought and everwet), period (fixed factor with 3 levels; first, second
185 and third drought) and treatment × period with a linear mixed-effects model. We used random
186 terms for plot, treatment nested in plot and period nested in plot (Supporting Information Table
187 S2a). Mid-day leaf water potential was analyzed as a function of treatment, period and treatment
188 × period with a linear mixed-effects model. We used random terms for plot, treatment nested in
189 plot and species (Supporting Information Table S2b).

190 Relative growth rate (RGR) was calculated based on a standardized height to account for
191 differences in seedling size across species and through time. To do this, RGR was analyzed as a
192 function of initial height at the start of each time-point (a continuous variable) and time-point
193 (fixed factor with 6 levels) with random effects for sub-plot nested within plot nested within
194 time-point and individual seedling. We applied an auto-regressive correlation structure to
195 account for the fact that a measurement of seedling height at a time-point is not independent of
196 seedling height at a previous time-point. From this analysis, we estimated RGR from the
197 extracted random term estimates for every seedling during each time-point while controlling for
198 height differences among seedlings (i.e. RGR calculated at the mean height of 60 cm; Supporting
199 Information Table S3a).

200 We tested the effect of treatments on the growth by analyzing these size-standardized
201 estimates of RGR as a function species (fixed factor with 20 levels), period (fixed factor with 2
202 levels; during and after rainfall exclusion shelters), year (fixed factor with 3 levels) and treatment

(fixed factor with two levels; everwet and drought). We also tested the two-way interactions of species × treatment, year × period and treatment × period as well as the three-way interaction of treatment × year × period. We used random effects for plot, treatment nested in plot, period nested in plot, year nested in plot, treatment nested in period nested in plot, treatment nested in year nested in plot, species nested in plot and species nested in treatment nested in plot (Supporting Information Table S3b). From this analysis, differences in RGR between drought and everwet treatments during the different temporal phases can be used to calculate resistance and recovery (i.e. the difference in RGR between seedlings in the drought and everwet plots during drought periods is resistance and after drought periods recovery). The difference in average growth between drought and everwet treatments over the entire year or over the entire experiment is therefore resilience as it encompasses both the resistance (drought) and recovery (post-drought) phases.

We also assessed average recovery of each species from the second and third year of drought (the average difference in growth between individuals in drought and everwet treatments after the removal of rainfall exclusion shelters) as a function of average resistance (the average difference in growth between individuals in drought and everwet treatments during rainfall exclusion shelters) using a linear model (Supporting Information Table S4) to test whether more resistant species recovered better. We removed the first year from this analysis because soil water availability was statistically indistinguishable between treatments in that year (Fig. 1a).

Probability of seedling survival was analyzed as a function of species, period, year, treatment, species × treatment, year × period, treatment × period and treatment × year × period with a binomial distribution (1 = alive and 0 = dead) and a complimentary log-log link function. We used random effects for plot, treatment nested in plot, species nested in plot, year nested in

plot and treatment nested in period nested in plot (Supporting Information Table S5). Furthermore, an offset, calculated as the natural log of the number of days since the last census divided by 30 (to assess survival on a monthly scale), was used to account for different time intervals between censuses. We also tested the effect of seedling size on survival by analyzing binomial survival as a function of average height throughout the experiment. We used random terms for plot and treatment nested in plot. All analyses were performed with the asreml-R package (ASReml 3, VSN International, UK) in the R statistical software (version 3.3.1; http://r-project.org).

**Results**

Soil water potential was significantly lower with rainfall exclusion shelters (-0.08 MPa, 95% CI: -0.1 to -0.06) than without (-0.01 MPa, 95% CI: -0.03 – 0.1). Although soil water potential was statistically indistinguishable between treatments in the first year, the difference between treatments increased with each following year that the exclusion shelters were applied (Fig. 1a). Leaf water potentials showed the same pattern as soil water potential (Fig. 1b) with seedlings under rainfall exclusion shelters having significantly lower water potentials (-0.61 MPa, 95% CI: -0.68 to -0.54) than seedlings without rainfall exclusion shelters (-0.48 MPa, 95% CI: -0.54 to -0.41). The increasing drought conditions with each year are likely due to improved methods of applying the rainfall exclusion shelters, increased competition in the communities as seedlings grew larger and required more water and lower rainfall during the period of exclusion in the second and third year (greater than 1200 mm in year one and less than 900 mm in year two and three).

Except for the first year when only marginal decreases in soil water were measured, RGR was significantly lower in the drought treatment when rainfall exclusion shelters were present

(i.e. resistance; difference in RGR between drought and everwet treatments in the second drought = -1.1e-04 cm $cm^{-1}$ $day^{-1}$, 95% CI: -1.3e-04 to -8.6e-05 and in the third drought = -2.8e-05 cm $cm^{-1}$ $day^{-1}$, 95% CI: -4.8e-05 to -7.8e-06; Fig. 2a). However, these significantly lower RGRs in the drought treatments switched to significantly higher RGRs after the rainfall exclusion shelters were removed (i.e. recovery; difference in post-drought RGR between drought and everwet treatments in the second year = 6.6e-05 cm $cm^{-1}$ $day^{-1}$, 95% CI: 4.5e-05 – 8.6e-05 and post-drought RGR in the third year = 8.7e-05 cm $cm^{-1}$ $day^{-1}$, 95% CI: 6.6e-05 – 1.1e-04; Fig. 2b). In year two, post-drought RGR only partially compensated for the reduction in RGR during the drought (post-drought RGR was 62% of the RGR reduction during rainfall exclusion shelters), but in year three, post-drought RGR overcompensated for the reduction in RGR during the drought (post-drought RGR was 310% of the RGR reduction during rainfall exclusion shelters). Therefore, annual RGR for seedlings in the drought treatment had significantly lower growth in year two but significantly higher growth in year three (i.e. resilience; Fig. 2c). Trends and differences were similar if the first year (when the drought treatments were not effective) was excluded from the analysis (Supporting Information Fig. S3).

The magnitude and direction of the effect of drought on RGR was significantly different among species (Fig. 3). Only three species had a significantly lower RGR during drought (Fig. 3a) while 13 species had a significantly higher post-drought RGR (Fig. 3b). However, if the first year is removed from the analysis (when soil water potential was only marginally reduced in the drought treatment; Fig.1a), then the number of species with a significantly lower RGR during drought increased to 13 species of the 20 species (Supporting Information Fig. S4). Regardless of these temporal variations in RGR, the overall differences in RGR between drought and everwet treatments over 3 years (i.e. multi-year resilience) were statistically indistinguishable from zero

for twelve species, exemplifying post-drought compensatory recovery (Fig. 3c and S4c). Therefore, even though intra-annual RGR was statistically different between drought and everwet treatments, average multi-year RGR was similar. Furthermore, recovery significantly increased with resistance across species (Fig. 3d) whereby more resistant species had better recovery. This analysis also showed that three species were overall negatively impacted by drought, and five species were overall positively affected by drought while all other species were compensating growth reductions during drought proportionally with increased post-drought growth.

Although seedling survival was high in both drought (86% survived; 33 seedlings died) and everwet (82% survived; 41 seedlings died) treatments, a cyclical pattern in probability of survival was observed in both treatments (Fig. 4a). The probability of survival was significantly higher during the period with rainfall exclusion shelters (February to July) than in the months that followed. Overall probability of survival was statistically indistinguishable between drought treatments (78% chance of survival per month, 95% CI: 67 – 88) than in everwet treatments (71% chance of survival per month, 95% CI: 60 – 82). We also tested the correlation between percent direct sunlight of a plot and the total number of seedlings alive at the last census for each treatment in each plot. Light was marginally positively correlated with total living seedlings for the everwet treatment (spearman rho = 0.51, P = 0.09) and was significantly correlated for the drought treatment (spearman rho = 0.62, P = 0.03). Species were significantly different in their survival with a range from 46% to 94% (Fig. 4b). Survival rates were lower for smaller seedlings (below 90% probability of survival for seedlings less than 56 cm tall, 95% CI: 83.4 – 89.8; Fig. S5), and seedlings that died were on average smaller than seedlings that lived (difference in height between dead and alive seedlings = 13.1 cm, 95% CI: 3.9 – 22.2).

## Discussion

Our yearly rainfall manipulation in an everwet tropical forest showed that seedlings subjected to recurrent drought can adjust their intra-annual growth rates while maintaining annual growth rates similar to communities under everwet conditions. Seedlings slowed their growth rates during drought and then increased growth rates in recovery periods when water availability was not limiting. Within the context of the four hypotheses proposed in the introduction — i.e. no effect, short-term reduction with compensatory recovery, short-term reduction and no compensating recovery or reduction and decline (Körner, 2006) — three species showed a reduced and declining growth rate with drought relative to everwet conditions, and twelve species showed an initial decline followed by a compensation that allowed recovery to similar growth rates of everwet conditions. Surprisingly, five species had an overall higher growth rate during resistance and recovery periods relative to seedlings in everwet conditions, which implies they benefited from imposed droughts likely due to reduced competition for light due to the negative effects on other species (i.e. potentially shading effects were reduced as a consequence of defoliation and slower growth in drought-impacted species). The probability of seedling survival followed a cyclical pattern with periods of higher and lower survival probability that was independent of soil water availability. We found that absolute survival was correlated with light, indicating low light superseded the effects of drought. Our results indicate that intra-annual plasticity in growth rates is a mechanism to compensate for reduced soil water availability and maintain annual and multi-year growth rates.

### *Intra-annual growth plasticity*

The plasticity of seedling growth under frequent inter-annual drought supports studies in other systems that found plant communities shift the timing of leaf, flower and fruit production

as a strategy in response to climatic changes in temperature and precipitation (Cleland *et al.*, 2007; Peñuelas *et al.*, 2012). Therefore, even in tropical forests with 20,000 years of fairly everwet conditions (Heaney, 1991; Bird *et al.*, 2005), tree species were able to temporally adjust functions to resist and recover from recurrent drought. One potential mechanism promoting this plasticity in growth may be an active shift from a growth to a storage strategy in response to water limitation (Wiley & Helliker, 2012). This response may also occur passively (Körner, 2015) as a consequence of plant growth being more sensitive to drought than photosynthesis (Muller *et al.*, 2011; Tardieu *et al.*, 2011), and as growth is inhibited by low water availability, photosynthesis continues causing photosynthates to passively accumulate. Regardless of whether active storage or passive accumulation occurs, this excess of nonstructural carbohydrates could be available for rapid growth at the onset of rainfall following a drought, and many of the species used in this experiment have been shown to accumulate nonstructural carbohydrates during drought (O'Brien *et al.*, 2014, 2015). In support of this argument, O'Brien *et al.*, (2015) showed that seedlings had reduced nonstructural carbohydrates under fluctuating water relative to regularly watered control seedlings but maintained growth similar to controls. Therefore, nonstructural carbohydrate dynamics may support recovery following drought.

An additional mechanism mediating this temporal shift in growth may be the negative effect of drought on soil microbial abundance and activity (Manzoni *et al.*, 2011; Vogel *et al.*, 2013; Maestre *et al.*, 2015) and, in turn, seedling access to soil nutrients (Sardans *et al.*, 2008; He & Dijkstra, 2014). During drought, nutrients may accumulate in the soil and then become available at the onset of rain and the return of soil microbial activity. Seedling competition may also contribute to the shift in growth rates. Drought may delay direct competition among seedlings for light and soil resources. In other words, seedlings achieved faster growth when

water was not limiting in drought treatments while seedlings in everwet conditions were growing continuously and directly competing earlier in time.

*Inter-specific differences in drought response*

Although seedling communities under drought conditions maintained annual growth rates at a similar level to those under everwet conditions, interspecific variation in resilience of growth was observed. Most species showed a neutral (12 species), or positive (5 species), growth response to frequent drought. The positive relationship between resistance and recovery suggests a shift in the competitive differences among species (Supporting Information Table S1). For example, the rank height of *Durio oxleyanus* dropped from 3 in everwet condition to 10 in drought conditions while *Shorea ovalis* moved from 19 in everwet conditions to 13 in drought conditions. We did not find a mechanism to explain this relationship (i.e. resistance, recovery and resilience were not correlated with functional traits such as wood density, nonstructural carbohydrates or specific-leaf area). These changes in growth rates may lead to shifts in demographic rates, but the effect on demographic rates is dependent on the interactions between more frequent drought and herbivores, pathogens and light that drive community assembly (Bell *et al.*, 2006; McDowell *et al.*, 2011; Lloret *et al.*, 2012; Bagchi *et al.*, 2014). However, direct tests of the interactive effects of drought and these factors will be necessary to understand vegetation shifts in a changing climate (Martinez-Vilalta & Lloret, 2016).

Three species showed overall negative responses to frequent drought with average growth rates significantly lower than that of seedlings in everwet conditions during both the resistance and recovery phase. These species were biologically distinct (i.e. each comes from a different family), suggesting that the factors which contributed to slower growth under drought were unique. *Koompassia excelsa* is a legume and may be particularly sensitive to decreases in

364 microbial activity inhibiting nitrogen fixation in nodules (Serraj *et al.*, 1999), which supports the
365 findings of Gei & Powers (2015) in tropical dry forests. The poorest performer under drought,
366 *Durio oxleyanus*, has already been shown to be highly sensitive to low soil water availability as a
367 result of its low nonstructural carbohydrate concentration in the stem and low wood density
368 relative to other species (O'Brien *et al.*, 2014, 2015). *Shorea macroptera* was one of the slowest
369 growing species regardless of the treatment, which contrasts previous work on this species which
370 found it to have intermediate growth rates (Philipson *et al.*, 2012, 2014). However, those studies
371 were carried out with limited or no seedling competition either within managed planting lines of
372 the Sabah Biodiversity Experiment (Philipson *et al.*, 2014) or in pots in controlled shade houses
373 (Philipson *et al.*, 2012). This difference may indicate that *S. macroptera* is unable to compete
374 well for limiting resources when seedling densities are higher. This diverse spectrum of species
375 showing a negative response suggests mechanisms underlying drought sensitivity were likely the
376 result of a complex interaction of variables (e.g. a suite of traits that confer resistance and
377 resilience) and not a single trait axis (O'Brien *et al.*, 2017).

378 *Survival rates*

379 Survival showed a cyclical pattern with periods of high survival followed by periods of
380 low survival throughout the 3 years. This cycle was surprising because of the aseasonal climate
381 of Borneo (Walsh & Newbery, 1999). However, rainfall was much greater from August to
382 January (6200 mm, period of low survival probability) than from February to July (5100 mm;
383 period of high survival probability) during the experiment (Fig. S1). There was also 100 fewer
384 rainless days and 26 more days with high rainfall (>30 mm in 24 hours) in the periods with low
385 probability of survival. This excessive rainfall may have enhanced mortality through poor abiotic
386 conditions in the soil or by promoting soil pathogen infection and spread.

387 There were only minor differences in mortality between treatments and therefore, little
388 evidence that mortality was mediated by drought. Light had a positive effect on survival, and
389 plots with less than 1% light had double seedling mortality (51 of 200, 26%) as compared to
390 plots with more than 1% light (23 of 280, 8%). These results support Philipson *et al.* (2014)
391 which showed a decrease in mortality with higher light. The cyclical mortality pattern may
392 represent thresholds in time whereby extended low light conditions cause a negative carbon
393 balance and lead to seedling death (Sevanto *et al.*, 2014; Hoch, 2015). Specifically, small
394 seedlings had lower survival rates than larger seedlings potentially due to being outcompeted by
395 larger seedlings for water or nutrients or shading by larger neighbors. Multiple variables are
396 likely contributing to this pattern and interacting with light including pathogens (Augspurger &
397 Kelly, 1984) and competition (e.g. density or size dependent mortality; Peters 2003).

398 In our manipulation of recurrent inter-annual drought, species responses in a tropical
399 aseasonal forest ranged from reduced to enhanced growth rates relative to everwet conditions.
400 Intra-annual fluctuations in growth followed rainfall patterns with reduced growth rates during
401 drought (i.e. resistance phase) and compensatory growth rates post-drought (recovery phase),
402 which maintained annual and multi-year growth similar to seedlings in everwet conditions (i.e.
403 resilience). Therefore, forest dynamics, and potentially vegetation shifts, under novel climate
404 conditions may be mediated by differences among species in their growth plasticity and not
405 solely by mortality rates, which indicates communities may be more robust to altered drought
406 regimes than predicted. These results suggest that even tropical forests with a historically
407 irregular, infrequent and weak drought regime can adapt to more frequent drought.

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**Author Contributions**

MOB designed and carried out the experiment, analyzed the data and wrote the manuscript. RO and GR provided conceptual development and logistical help for working in Sabah, Borneo.

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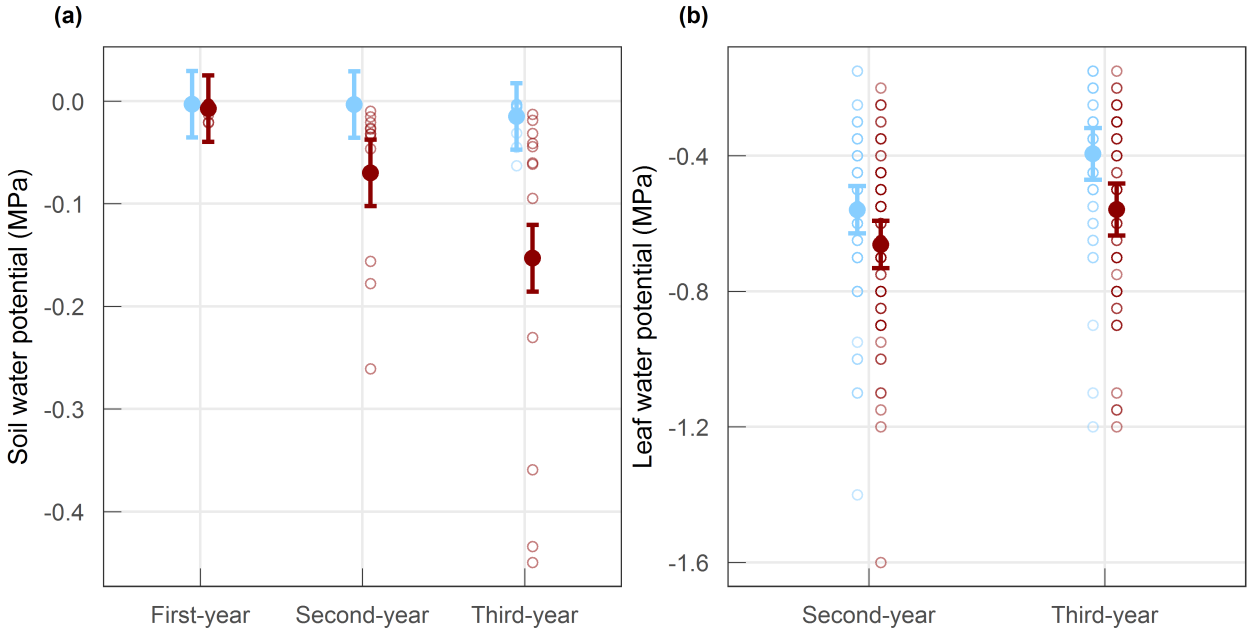
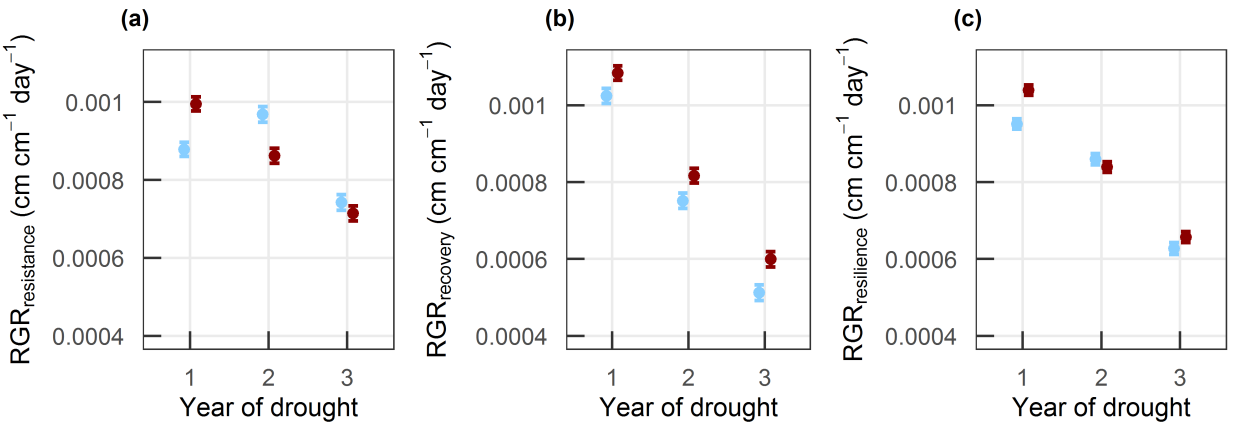
557 **Supplementary Information**

564 Fig. S2. Light levels in each plot.
565 Fig. S3. Replicate of Fig. 2 without first year of drought.
566 Fig. S4. Replicate of Fig. 3 without first year of drought.
567 Fig. S5. Relationship between seedling height and survival.



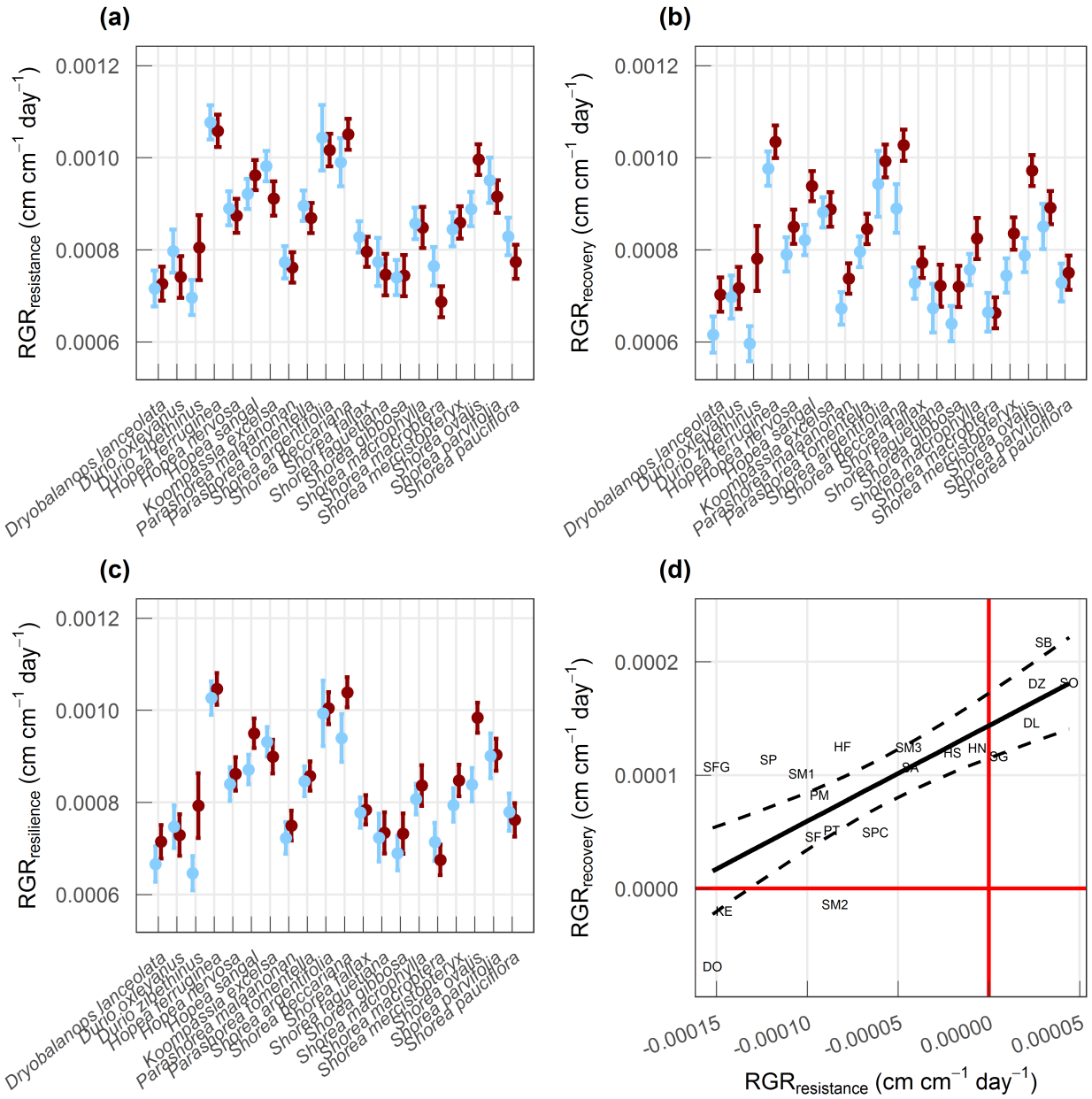

568

569 **Fig. 1 Mean soil water potential and minimum leaf water potential during rainfall**
570 **exclusion periods.** (a) Soil water potential (95% CI) modelled from volumetric water content
571 using the filter paper method for everwet (blue) and drought (red) treatments. (b) Mid-day leaf
572 water potential measured after approximately 75 days of rainfall exclusion for the second and
573 third year of drought.




574

575 **Fig. 2 Relative growth rate (RGR) for everwet and drought treatments.** (a) RGR (95% CI)
576 was significantly lower in drought (red) than everwet (blue) treatments when rainfall was
577 excluded for the second and third year (i.e. the resistance phase). The first year likely showed a
578 different pattern because the rainfall exclusion shelters were not effective at achieving significant
579 differences in soil water that year (Fig 2a). (b) Following the removal of rainfall exclusion
580 shelters (i.e. the recovery phase), drought treatments grew significantly faster than everwet
581 treatments. (c) Average annual RGR (i.e. resilience of each year) for seedlings in the drought
582 treatment had significantly lower RGR in year two but significantly higher growth in year three.
583 The observed RGRs were removed for readability.




584

585 **Fig. 3 RGR during and after rainfall exclusion for all species.** (a) Mean RGR (95% CI)
586 during periods of rainfall exclusion shelters (resistance) was highly variable among species with
587 some showing significantly faster growth in drought (red) than everwet (blue) treatments while
588 others were showed significantly slower growth. (b) Mean RGR after periods of rainfall
589 exclusion shelters (recovery) was also highly variable among species. (c) This intra-annual
590 variability led to statistically indistinguishable RGR between drought and everwet treatments for

most species over the 3.5 years of the experiment (resilience). (d) Recovery significantly increased with resistance. Three species showed overall negative effects of drought, twelve species showed proportionally compensatory effects whereby faster growth after drought offset slower growth during drought and five species showed overall positive effects. Species codes are the first letter of genus and specific epithet (Table S1).

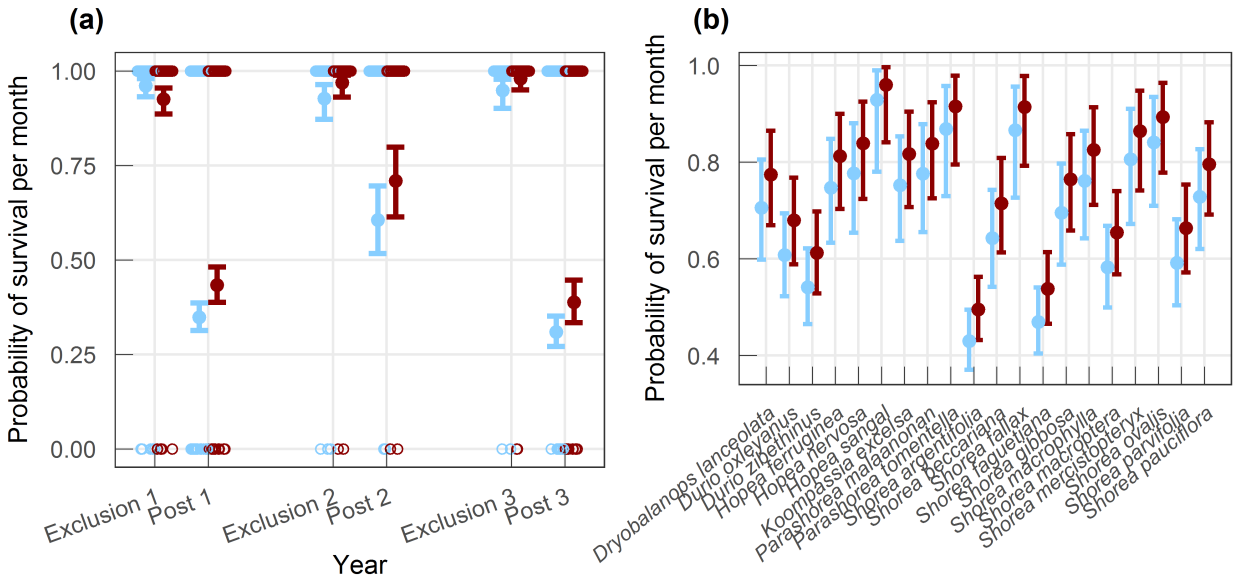



**Fig. 4 Survival trends at the treatment and species level.** (a) Probability of survival (95% CI) was higher in drought treatment during all time periods except the first period with rainfall exclusion, but average probability of survival over the entire experiment was not significantly different between drought and everwet treatments (Table S5). Interestingly, we found a cyclical trend with more death occurring between August to January than from February to July. (b) Similar to growth, species were highly variable in their probability of survival.